

## THE FAMILY TRIPHORIDAE AND ITS SYSTEMATIC POSITION

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## ABSTRACT

The Triphoridae have hitherto been referred to the Cerithioidea because of certain shell characteristics, although some recent authors have pointed out that the family differs from others of that superfamily in radula, alimentary tract and operculum. This paper deals with 16 Japanese species which are placed into 3 groups, according to their radulae and opercula. Together with another group reported by Risbec (1943), 4 groups are recognized within the family.

The 1st of these groups has a multispiral operculum. The radular formula is 8-5·1·1·1·5-8. The rachidian and lateral teeth are multicuspid, the marginals unicuspid. This group is represented by the common European *Triphora perversa*, the South American *T. nigrocincta*, the Japanese *T. otsuensis*, and some Japanese species of *Notosinister*.

The 2nd group of the family has the same operculum as the first, but its radular formula is 7·6·3·6·7. Three pentacuspoid rachidians are flanked by 6 lateral teeth, which differ from them only in having 3 cusps. The marginal teeth are unicuspid as in the 1st group. A New Caledonian species, *T. montrouzieri*, and another undetermined species of *Triphora*, reported on by Risbec, are members of this 2nd group.

The 3rd group has the same type of radula as the 2nd group in both number of teeth and cusps on each tooth, but the operculum is comparatively paucispiral (5 whorls), thereby differing from the former 2 groups. This group includes forms with the "three-mouthed type" of aperture, such as *Iniforis concors* and *I. albogranosa*, common to the Indo-Pacific area.

The 4th group has a comparatively paucispiral operculum similar to that of the 3rd group. Its radular formula is  $n \cdot 1 \cdot 1 \cdot 1 \cdot n$  ( $n=9-30$ ); the rachidian tooth has 3-5 cusps, the lateral is quadricuspoid, and the marginals have 2-3 cusps. The majority of species of *Mastonia*, *Inella*, *Litharium*, *Cautotriphora* and *Viriola* are included in this group.

In this paper, the hithertoknown triphorid genera and sections are reviewed. A number of forms have been rearranged from the viewpoint of anatomy and shell into 3 new subfamilies: the Triphorinae (group 1), the Iniforinae (groups 2 and 3) and the Mastoniinae (group 4), of which the Triphorinae are considered the most primitive and the Mastoniinae the most advanced. Eleven genera are recognized and a new genus, *Risbecia*, is proposed for "*Triphora*" *montrouzieri*.

According to features of their digestive tracts, such as the acrembolic proboscis, the presence of an oesophageal pouch, their radulae and the spiral (not lamellate) opercula, it is not appropriate either to retain the family Triphoridae in the essentially taenioglossid superfamily Cerithioidea or to place it in the neogastropod suborder Stenoglossa. For these reasons the author has already established a new superfamily Triphoroidea in the order Mesogastropoda. This newly proposed superfamily is placed closer to the superfamily Epitonioidae. Furthermore, a new suborder, the Heterogastropoda, (Habe et Kosuge, 1966), which includes the Triphoridae, Mathildidae, Architectonicidae and Epitonioidae (Ptenoglossa), is distinguished from both the Taenioglossa and Stenoglossa.

## INTRODUCTION

Triphorid snails usually live in the intertidal zone of rocky shores or coral reefs of tropical to temperate regions, but some are known to live on the ocean bottom up to depths of 500 m, or in arctic seas. They are frequently found on various sponges such as *Halichondria*, on which they crawl, or in which they partly or completely bury themselves. In such a habitat they feed on tissues of the sponge, and have large numbers of monotonous, siliceous spicules in their digestive tracts. Observations on Japanese triphorids suggest that they normally eat only sponges.

The family Triphoridae is the only typically sinistral group among the marine Gastropoda, and the arrangement of the organs in the mantle cavity and of the nervous system is a reversal of that occurring in the dextral gastropods.

Members of the family Triphoridae are easily recognized by their subulate or somewhat inflated conical spires and their sinistrally coiled shells, features which, except for a few dextral Tertiary fossil species (*Triforis*) of doubtful status, from the Paris Basin, are constant for the family.

The shell form in the Triphoridae is more or less elongate; some species have a subulate, long spire, but other species have short inflated and spindle-shaped spires. The shells are generally small, but there is considerable variation in the relative sizes of the various species, ranging from 3-40 mm or more in their adult form.

There are a few outstanding characters by which genera and subgenera can be easily recognized and separated. These

characters are mainly shell sculpture, the protoconch, radulae and opercula.

The shell sculpture consists of a few smooth spiral ridges or granulate rows on each whorl. Usually there are a few rows of rounded or spirally elongated granules, which are very often connected by spiral and axial costae. But, in a few species, there are 2 or 3 smooth spiral ridges, which are sometimes mixed with a granulated spiral row.

Anatomical studies of the family are rather scanty and relatively recent. In the present paper a systematic scheme within the family is proposed which takes into consideration all known features (in particular the radulae and opercula) in conjunction with the shell.

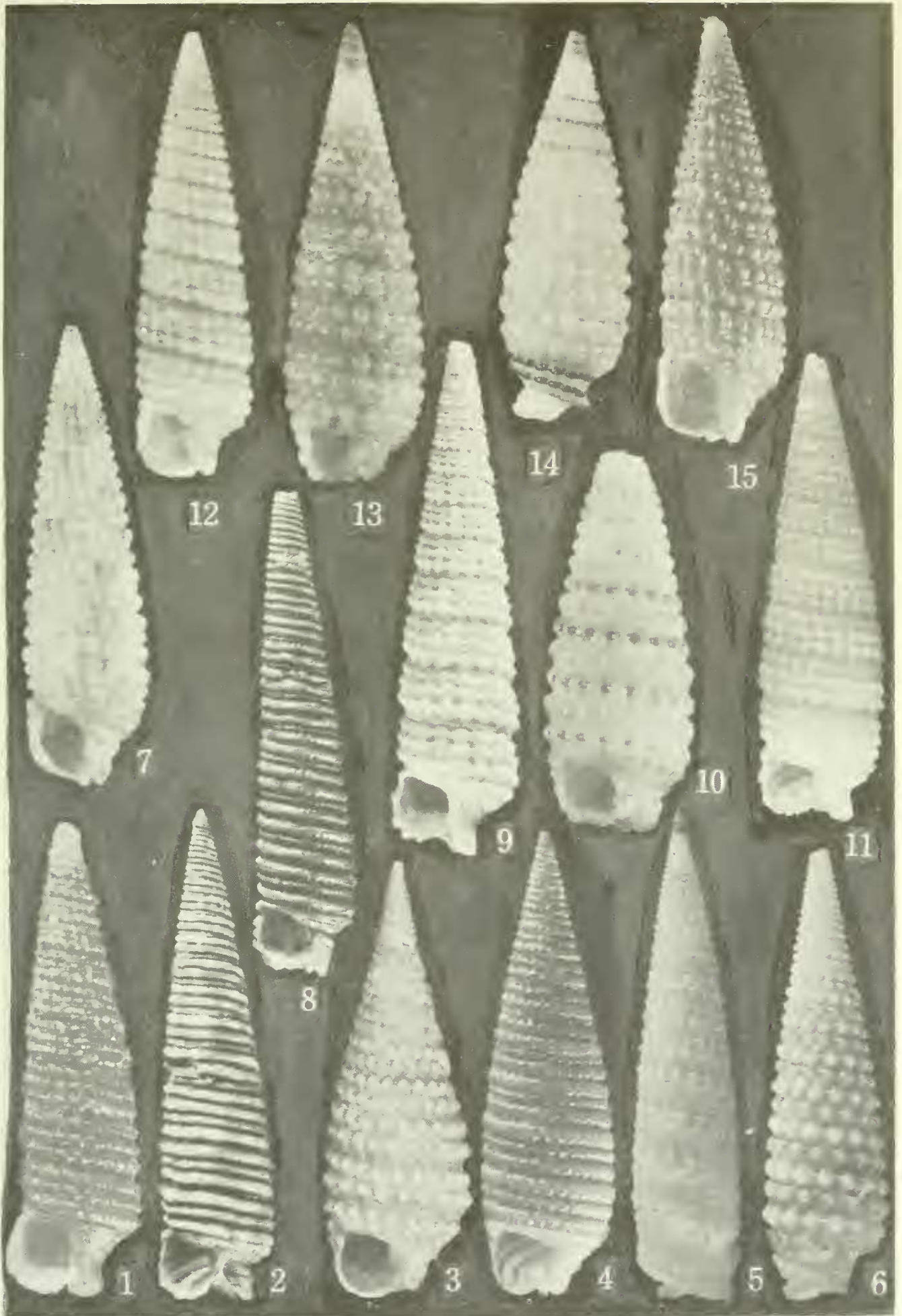
## MATERIALS AND METHODS

The anatomical data in this paper principally concern *Mastonia limosa*, which is described in detail. For 15 other Japanese species belonging to 7 genera, the data concern mainly the radulae and opercula, because the anatomy of these species was found to be very similar to *M. limosa*.

The radulae were prepared and studied in detail by mounting them unstained in glycerin jelly. Only fully formed teeth were included in the count of radular rows. Teeth 1/2 the size of the majority in the radular ribbon were considered nascent. Gross anatomy of each species was studied. At least 3 animals of each species, preserved in 70% alcohol without previous relaxation, were dissected in order to gain a concept of the relations of the organs. The terminology of the soft parts is primarily that of Fretter & Graham (1962).

## PLATE I. Shells of some Japanese Triphoridae (X8)

1. *Litharium kurodai* (Kosuge); 2. *Viriola connata* (Montrouzier); 3. *Mastonia rubra* (Hinds);
4. *Cautotriphora pavimenta* (Laseron); 5. *Iniforis concors* (Hinds); 6. *Iniforis albogranosa* (Kosuge); 7. *Mastonia conspersa* (Smith); 8. *Viriola tricincta* (Dunker); 9. *Cautotriphora alveolata* (Adams & Reeve); 10. *Mastonia monilifera* (Hinds); 11. *Cautotriphora hervieri* (Kosuge);
12. *Triphora otsuensis* (Yokoyama); 13. *Mastonia undata* (Kosuge); 14. *Mastonia ustulata* (Hervier); 15. *Cautor hungerfordi* (Sowerby).



## HISTORICAL REVIEW

Although conchological studies of the Triphoridae were begun long ago, there have been only a few anatomical investigations or systematic studies based on valid premises. Fischer (1887) reported on the radula of *Triphora perversa* (Linnaeus), a species commonly found in the European and Arctic seas. Its radular formula was reported to be 8·1·1·1·8. Shapes of the radular teeth were shown more exactly by Fretter (1951). Risbec (1943) dissected *T. montrouzieri* (Hervey) and another undetermined species of *Triphora*, and described their digestive organs and radulae. The formula for these 2 species was reported as  $n' \cdot n \cdot 3 \cdot n \cdot n'$  ( $n=5$  or  $7$ ,  $n+n'=13$ ). Fretter (1951) presented a detailed report on the interesting relationships between the oesophagus and the opening of the salivary duct in *T. perversa*, and pointed out certain similarities with the stenoglossan Buccinoidea, especially in the oesophageal pouch. Johansson (1953) closely examined the genital organs of *T. perversa*, making observations which were inconsistent with those of Fretter in many respects. For example, he pointed out that the glandular pallial oviduct, which was described by Fretter as an open groove, is actually a wholly closed canal throughout its length.

Risbec (1955) noted that the Triphoridae differed from the other "cerithiids" in radulae and digestive organs. He judged the triphorids to be more closely related to the stenoglossan family Columbellidae (Buccinoidea) than to the Cerithioidea and he believed that a new group should be created, intermediate between the Mesogastropoda and the neogastropod Stenoglossa. Taylor & Sohl (1962), unable to allocate them to a suitable place, list them in the Cerithioidea.

Marcus & Marcus (1963) examined *Triphora nigrocincta* (C. B. Adams) and figured its genital organs and radula. The radular formula and shape of the teeth are closely similar to those of *T. perversa*. Kosuge (1964), studying

10 triphorid species from the Japanese area, reported 2 different forms of radulae and opercula, and established a new superfamily, Triphoroidea, in the Mesogastropoda. One form of radula and a multispiral operculum was found in *Triphora otsuensis* and 2 undetermined species of the genus *Notosinister*; another form and relatively paucispiral opercula in *Mastonia rubra* and other 6 species of Mastoniinae. These features are re-described precisely in this paper. This author has now carefully reviewed the former studies and in the present paper presents a more definitive systematic treatment of the family.

In this and the following paragraphs, the nominal triphorid genera occurring in the literature are reviewed. Since Blainville (1828) first established the genus *Triphora* as a taxon of cerithiid molluscs, over 50 generic or subgeneric names have been placed in the family. The name *Triphora* has been regarded as a synonym of *Triforis*, which was originated by Deshayes (1834) for a fossil species from the Eocene Paris Basin. *Triforis* was later erroneously considered to date from 1824 and, accordingly, the name *Triforis* had been widely considered to have priority in the family. However, later investigations have shown that the genus *Triforis* can no longer be considered representative for the family. If maintained, it must be restricted to a minor group typified by the Eocene dextral fossil *T. plicata* Deshayes. *Tristoma* was established by Menke (1830) as a subgenus of *Triforis*.

Hinds (1843) named 3 subgenera (treated as genera by latter authors: *Ino*, *Sychar* and *Mastonia*) and many species. Since *Ino* is preoccupied by an entomological generic name (Leach, 1815), Bayle (1878) proposed a substitute name, *Inella*. Jousseume (1884) established 7 new genera: *Trituba*, *Iniforis*, *Mastoniaeforis*, *Stylia*, *Metalepsis*, *Euthymia* and *Viriola*. The genus *Euthymia* is preoccupied (Stål, 1876), and Thiele (1931) proposed a substitute name, *Euthymella*. Bucquoy, Dautzenberg & Doll-

fus (1884) established *Biforina* as a subgenus of *Triforis*. Harris & Burrows (1891) proposed *Ogivia* and *Epetrium* as generic names for European triphorid fossils. Oliver (1914) established the genus *Sinistroseila*, with the type species *T. incisa* (Pease). Dall (1924) established 2 genera on the nature of their protoconch, *Strobiligera* and *Litharium*. Finlay (1927), in treating the Triphoridae of New Zealand, recognized 3 new genera, *Notosinister*, *Cautor* and *Teretriphora*.

Cotton & Godfrey (1931) summarized the South Australian Triphoridae, maintaining Finlay's genera and also naming 3 new genera, *Eutriphora*, *Isotriphora* and *Hypotriphora*. Thiele (1931) recognized 8 genera in his Handbuch der systematischen Weichtierkunde: *Triphora*, *Litharium*, *Inella*, *Iniforis*, *Euthymella*, *Mastonia*, *Viriola* and *Sychar*. He treated *Tristoma*, *Biforina* and *Notosinister* as synonyms of *Triphora*, and *Mastoniaeforis* as a synonym of *Mastonia*. He ignored the other nominal genera and subgenera. Vayssi re (1931) proposed the name *Sinusigera dautzenbergi* for a larval stage of *T. perversa*. Wenz (1938) used only 4 generic names, *Triforis*, *Triphora*, *Viriola* and *Sychar*. He restricted *Triforis* to a fossil group and subdivided it into 3 sections: *Trituba*, *Epetrium* and *Triforis* (s. str.). He included 13 sections in *Triphora*: *Triphora* (s. str.), *Eutriphora*, *Notosinister*, *Cautor*, *Isotriphora*, *Teretriphora*, *Hypotriphora*, *Sinistroseila*, *Ogivia*, *Litharium*, *Inella*, *Euthymella* and *Mastonia*. *Tristoma* and *Biforina* were considered synonyms of *Inella*. Laws (1940) in treating the fossil Mollusca of New Zealand, proposed a new subgenus, *Cautotriphora*, for the genus *Notosinister*. Olsson & Harbison (1953) established 2 new Pliocene fossil subgenera, *Cosmotriphora* and *Cinctriphora*, for the genus *Triphora* in southern Florida. Laseron (1954), in his paper on the Triphoridae of New South Wales, Australia, recognized the genera *Notosinister*, *Isotriphora* and *Teretriphora*,

and named 2 additional genera, *Solosinister* and *Magnosinister*. This same author (1958) established 13 new genera: *Contraforis*, *Epiforis*, *Orbitophora*, *Opi-maphora*, *Nanaphora*, *Coriophora*, *Aclophora*, *Distophora*, *Liniphora*, *Mesophora*, *Subulophora*, *Tetraphora* and *Torresophora* in his paper on North Australian Triphoridae. In addition, he recognized the following 8 previously named genera: *Iniforis*, *Triphora*, *Mastoniaeforis*, *Sychar*, *Viriola*, *Inella*, *Euthymella* and *Mastonia*.

Kosuge (1961-63), in adopting Laseron's system, recognized and used the following 17 genera and subgenera for the Triphoridae of Japan: *Triphora*, *Sychar*, *Viriola*, *Inella*, *Euthymella*, *Mastonia*, *Notosinister*, *Tetraphora*, *Isotriphora*, *Cautor*, *Contraforis*, *Iniforis*, *Epiforis*, *Orbitophora*, *Teretriphora*, *Liniphora* and *Distophora*.

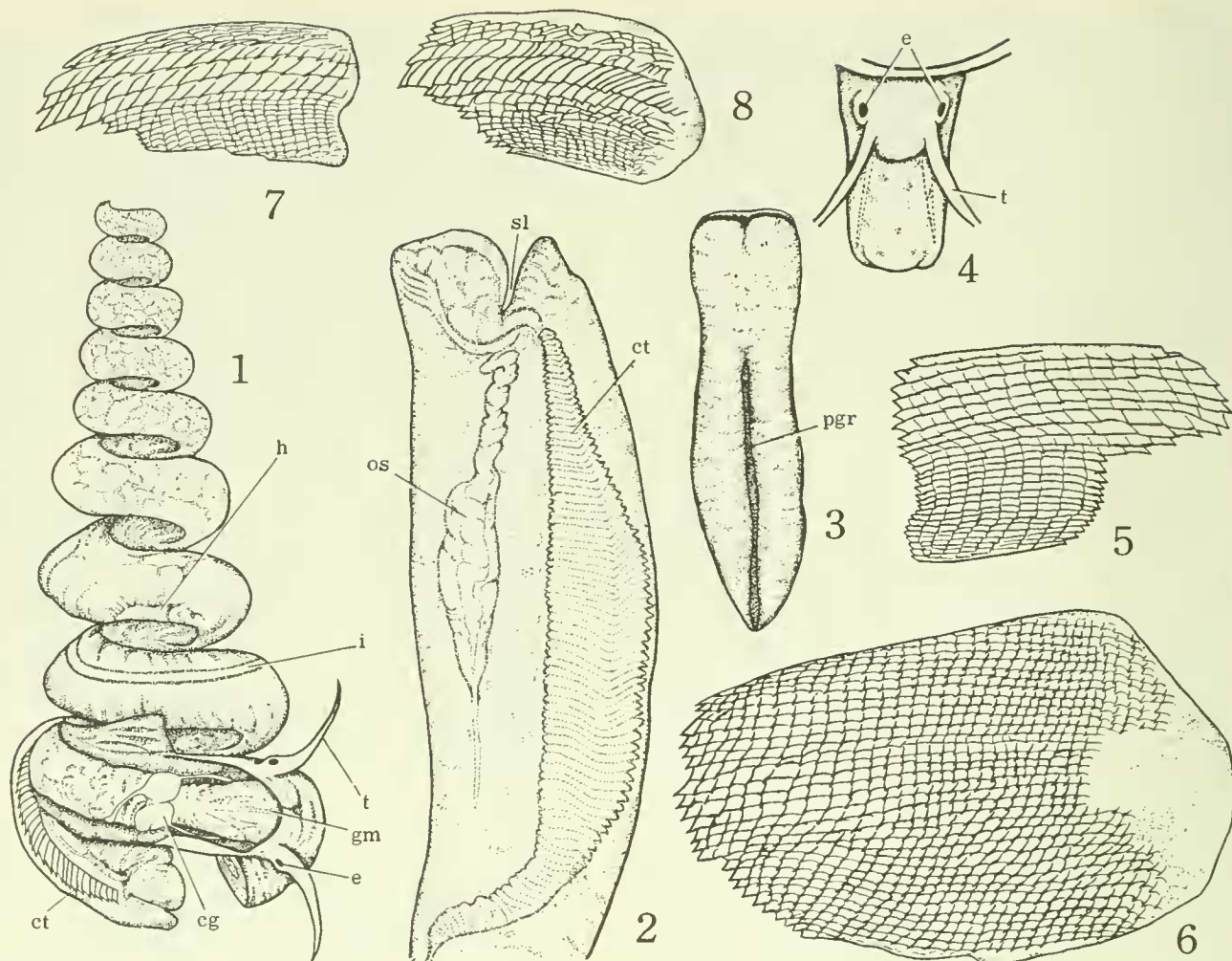
## OBSERVATIONS

### Anatomical features of some Japanese Triphoridae

*Mastonia limosa* Jousseume, 1884.  
(Figs. 1-5, 9-20)

The horny, brownish, paucispiral operculum has 5 whorls. The rather large foot (Fig. 3) is truncated in front and tapers to a blunt point posteriorly. A longitudinal pedal groove runs along the mid-line of the sole, becoming gradually deeper and wider towards its posterior end. The pedal mucous glands open into this groove and secrete abundant amounts of mucous threads, which are used as a climbing rope or to secure the animal on wave-swept rocks. The epipodial wall is yellowish-white with opaque spots.

The tentacles (t, Figs. 1, 4) are slender and have the same coloration as the epipodium. The eyes (e, Figs. 1, 4) are black and are situated near the base on the outside of the tentacles. There is an oval cuticular lens in the cavity of the eye. The retina is formed by black pigmented cells, which are easily



FIGS. 1-4. *Mastonia limosa* (Jousseau). FIG. 1. Body with shell removed; mantle and body wall cut open dorsally in body whorl. FIG. 2. Ctenidium and osphradium. FIG. 3. Ventral view of foot. FIG. 4. Anterior part of head.

FIGS. 5-8. Squamate jaw plates of some Triphoridae (X370). FIG. 5. *Mastonia limosa*. FIG. 6. *Cautotriphora alveolata*. FIG. 7. *Iniforis albogranosa*. FIG. 8. *Viriola tricincta*.

LIST OF ABBREVIATIONS IN TEXT FIGS. 1-20

au	auricle	oep	oesophageal pouch
ba	bulbus aortae	os	osphradium
bc	buccal cavity	orn	oral nerve
bg	buccal ganglion	pg	pedal ganglion
cg	cerebral ganglion	pgr	pedal groove
cpc	cerebropedal connective	plpc	pleuropedal connective
cplc	cerebropleural connective	pr	proboscis
ct	ctenidium	prg	propodial ganglion
e	eye	r	radular ribbon
ebv	efferent branchial vein	rm	retractor muscle
env	efferent vein of nephridial gland	rplg	right pleural ganglion
gm	gelatinous mass	sgl	salivary glands
h	heart	sl	slit in mantle
i	intestine	soe	sub-oesophageal ganglion
j	jaw plate	spoe	supra-oesophageal ganglion
k	kidney	st	stomach
lplg	left pleural ganglion	ve	ventricle
mf	muscle fibre (not nerve)	t	tentacle
oe	oesophagus	tn	tentacular nerve

stained with hematoxylin.

Because of the sinistral coiling of the animal, the ctenidium and osphradium are situated on the right side, and the rectum and pallial oviduct are on the left side, an orientation that is just the opposite of that found in dextral gastropods. There is a narrow dorsal slit (sl, Fig. 2) on the right side of the mantle. The inner surface of the mantle is smooth on the right side, while there are many folds on the left side. The ctenidium (ct, Figs. 1, 2) is rather short in proportion to the length of the pallial cavity, and ends on the right side at about 1/2 the length of the cavity. An efferent branchial vessel may be traced back from the posterior end of the ctenidial axis to the heart. Each of the approximately 54 leaflets of the ctenidium (Figs. 13, 14) is small and has a low triangular shape. The osphradium (os, Fig. 2) runs along the right side of the ctenidium, parallel to its axis and is almost the same length as the ctenidium. The osphradium is a narrow, yellow, pigmented ridge, which has a shallow groove on the mid-line of the dorsal surface; it consists of 2 cell layers, the outer one consisting of rod-shaped cells that contain yellow pigment. The inhalent current passes into the pallial cavity on the right side through the rather tubular mantle edge. The strong exhalent current leaves on the left side. There are long, rod-shaped processes on the left side of the mantle edge and the body wall, the so-called "pallial tentacles"; their surface is covered by conspicuous cilia, which assist in producing the exhalent current. These interesting structures are found in the rissoid snails and may have the same characteristics as those found in the Ptenoglossa and Opisthobranchia, but they do not occur in the cerithiids. The hypobranchial gland is broad, thick, dull white and semi-transparent. It becomes thicker and broader toward its posterior end.

#### Alimentary tract

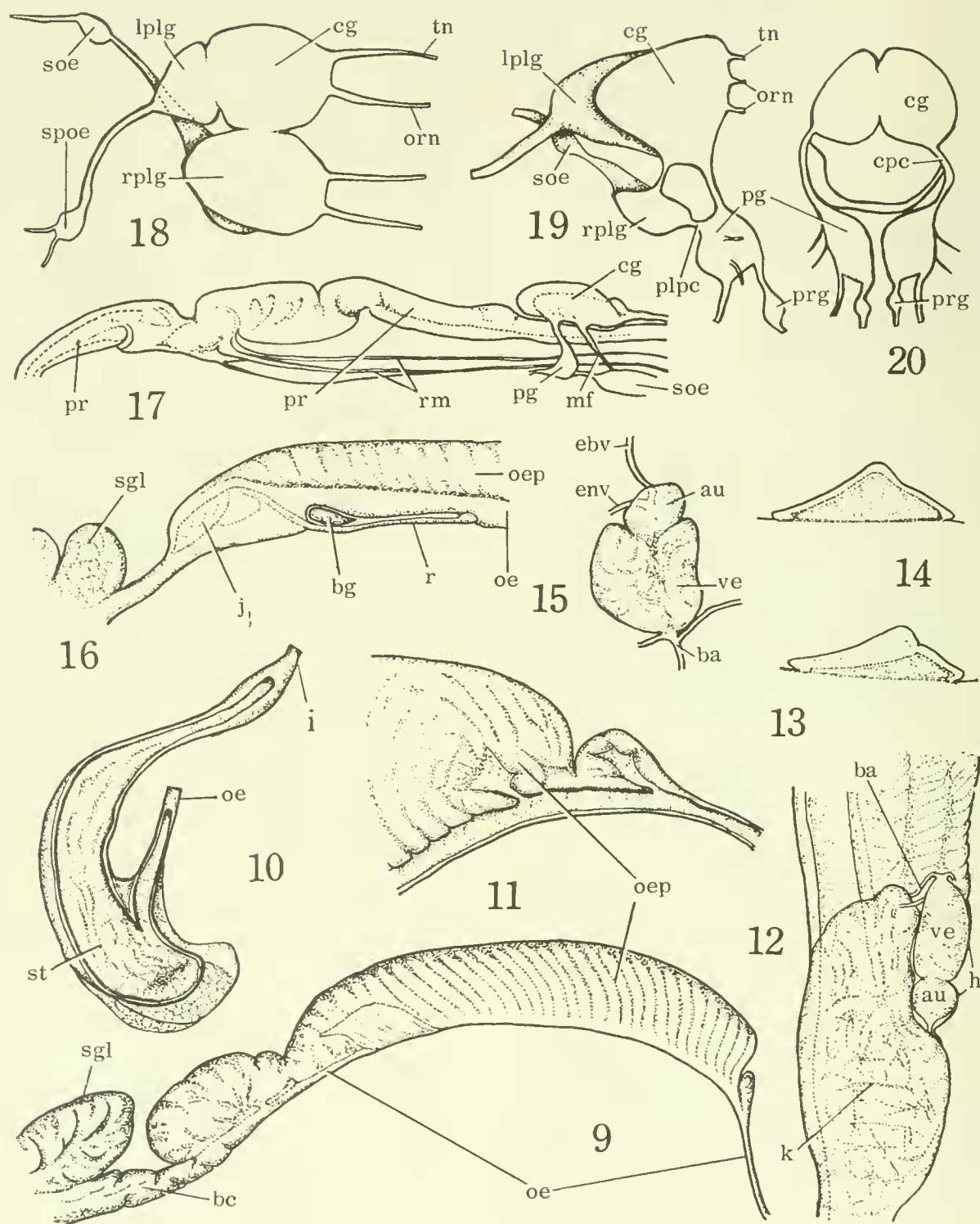
A gelatinous, very large, opaque-

white, soft mass (gm, Fig. 1), which almost fills the anterior part of the head, lies between the mouth opening and the cerebral ganglia. Its cells are large and similar to mucus cells. The long muscular proboscis (pr, Fig. 17) continues from this swelling and extends posteriorly. When it introverts, it passes through the constricted oesophageal nerve ring and comes to lie in the first whorl of the shell. The buccal cavity is then situated in the terminal part of the proboscis and is not expanded. The jaw (j, Fig. 16) is attached at the anterior tip of the buccal cavity and is covered on the top by the radular ribbon. It consists of a pair of wing-shaped plates (Fig. 5) which are joined on their dorsal edges. Each of these plates is covered with numerous elongate-quadrangular scales with aculeated tops.

The radular ribbon (r, Fig. 16) is not long, only about 3x the length of the buccal cavity; 2/3 of it lie in the radular sac. The radular sac extends along the oesophagus and has a weak swelling at its end. Each transverse radular row contains 37 very minute teeth, of the formula  $17 \cdot 1 \cdot 1 \cdot 1 \cdot 17$ . The rachidian tooth attains a width of  $1.8\mu$  and a height of  $1.2\mu$ . It has 3 cusps, of which the central one is larger. The lateral tooth is somewhat larger than the rachidian and has 4 cusps of equal size. The marginal teeth are smaller than the others and are bicuspid (Fig. 33a, b, c).

The oesophagus is looped at the end of the radular sac and extends to the stomach. The salivary glands (sgl, Figs. 9, 16) lie on the dorsal side, ranging from the tip of the proboscis to the anterior part of the oesophagus. On the animal's right side, secretion from the salivary glands is poured out by a duct leaving the glands at a point 1/3 the distance from the anterior end, and entering the anterior part of the oesophagus.

An oesophageal pouch (oep, Figs. 9, 11, 16) runs dorsally along the mid- and posterior 1/3 of the oesophagus, and opens into the oesophagus at the end



FIGS. 9-20. *Mastonia limosa* (Jousseau). FIG. 9. Oesophageal pouch. FIG. 10. Stomach. FIG. 11. Oesophageal pouch (sagittal section). FIG. 12. Heart and kidney. FIGS. 13, 14. Leaflets of ctenidium. FIG. 15. Heart. FIG. 16. Buccal cavity. FIG. 17. Anterior part of proboscis. FIGS. 18-20. Cephalic ganglia. FIG. 18, dorsal view; FIG. 19, lateral view; FIG. 20, frontal view.



of its posterior part; it is an expanded gland, forming a series of transverse folds which subdivide the lumen. Each fold consists of 2 layers, with a narrow space between them, which are separated from each other by a thin membrane.

The stomach (st, Fig. 10) lies entirely in the visceral mass, mainly on the outer side towards the animal's right; it is an elongated smooth pouch extending through more than 2/3 of a spiral whorl. The oesophagus (oe, Fig. 10) opens into it about half way between its 2 ends. The intestine (i, Fig. 10) leaves the topographically anterior end of the pouch, whose opposite, posterior end is blind. Internally the cavity of the anterior half of the stomach is weakly crenated and the duct of the digestive gland opens into it.

The intestine (i, Fig. 1) runs from the right side of the body across to the left in a C-shaped loop and enters the left side of the mantle, along which it passes anteriorly to open at the anus. The initial part of the intestine slightly swells and then narrows; the remainder is rather broad. The rod of faecal matter is segmented into spindle-shaped pellets, which mainly consist of sponge spicules.

#### The excretory organ

The kidney (k, Fig. 12) is a small corrugated mass that lies on the right side of the visceral mass and abuts against the upper end of the mantle cavity. It opens into that cavity by a very narrow slit-like aperture. It lies next to the heart and a part of the genital duct.

#### Circulatory system

The heart (h, Fig. 12; Fig. 15), lying within the coelomic pericardial cavity along the right side of the visceral mass, anterior and ventral to the kidney, is in contact with the innermost end of the pallial cavity. The auricle (au) is connected with the ctenidium through a long efferent branchial vessel (ebv) along the right edge of the cavity. The anterior

aorta runs forward on its way to the head and foot.

#### Nervous system

The nerve ring lies behind the gelatinous oral mass (gm, Fig. 1) which fills the initial part of the proboscis. The cerebral ganglia (cg, Figs. 17-20) are connected to one another by the cerebral commissure, and to the pleural and pedal ganglia by connectives. They are large and lie close together, giving off the ocular, tentacular and oral nerves (tn, orn, Figs. 18-19). The left pleural ganglion (lplg, Figs. 18, 19) lies close behind, and a little ventral to the left cerebral ganglion. The right pleural ganglion (rplg, Figs. 18, 19) lies under the right cerebral ganglion. The pleural ganglia are slightly smaller than the cerebral ganglia and are connected to the pedal ganglia by pleuro-pedal connectives (plpc, Fig. 19), which run alongside the cerebropedal connectives (cpc, Fig. 20). The left pleural ganglion gives rise to a connective, running along the dorsal side of the proboscis, to the supra-oesophageal ganglion (spoe, Figs. 17, 19). This latter ganglion lies on the right and gives off a connective to the visceral ganglion; it is also the origin of the branchial and osphradial nerves. The right pleural ganglion gives rise to a connective which runs along the ventral side of the proboscis to the suboesophageal ganglion (soe, Figs. 17-19) lying on the left. The arrangement of the nerves is the reverse of that found in dextral gastropods.

The pedal ganglia (pg, Figs. 19, 20) are slightly smaller than the cerebral ganglia. Anterior and posterior main nerves arise from both pedal ganglia. The antero-pedal nerves have a small propodial ganglion (prg, Figs. 19, 20) at their base. Each of the pedal ganglia also gives rise to nerves to various parts of the foot. The buccal ganglia (bg, Fig. 16) are located laterally of the buccal cavity at the point where the oesophagus and the radular sac originate from the buccal cavity.

## Reproductive organs

### 1) *Female tract*

In the female, the sperm collecting duct opens at the terminal end of the mantle cavity. It is joined to the bursa copulatrix, which is situated between the kidney, intestine and body wall. The bursa copulatrix is extremely large and pupa-shaped and broader at its posterior part. This pouch on the one hand receives the sperm collecting duct and on the other gives off a narrow duct to the receptaculum seminis, running parallel to the sperm collecting duct. The receptaculum seminis is a small semitransparent pouch that is connected to the ovary by a narrow oviduct. The ovary is tessel-shaped and lies in the visceral hump. After joining with receptaculum seminis, the oviduct runs forward to the mantle cavity and continues as the glandular oviduct; at the point where it crosses the intestine a broad blind sack extends at its upper end. The glandular oviduct coils and continues downwards along the left side of the intestine to the female pore near the anus. In the terminal part of its course it is a circular tube surrounded by semitransparent mucus glands.

### 2) *Male tract*

The testis resembles the ovary in appearance; the tubules of the testis lead into the testicular duct which runs towards the mantle cavity. The duct then narrows and extends along the left side of the intestine, opening near the anus. Since a penis is missing, the spermatheca are conveyed directly to the female mantle cavity.

The gross anatomy of the soft parts, is essentially the same in all 16 Japanese species examined; for this reason it is not redescribed in the following 15 species, which are defined primarily on the basis of their radulae and opercula. Some anatomical features when distinctive, are indicated.

*Mastonia rubra* (Hinds, 1843) (Pl. 1,

Fig. 3; Text figs. 26a, b, c)

The operculum is horny and paucispiral. The pentacuspoid rachidian tooth is bordered on each side by quadricuspoid lateral teeth and tricuspoid marginals; the radular formula is 12·1·1·1·12. In general, radular characteristics of this species are close to *Mastonia limosa*, except for the greater number of cusps on the rachidian (5 vs. 3) and marginals (3 vs. 2) (see pattern typical for Mastoniinae, Fig. 33).

*Mastonia undata* (Kosuge, 1962)

(Pl. 1, Fig. 13)

The operculum is horny and paucispiral.

The osphradium is thick and broad. The cerebral ganglia are rather large in proportion to the head. The looping area of the oesophagus is rather short.

The radula consists of a tricuspoid rachidian tooth, the quadricuspoid laterals and bicuspid marginals. The radular formula is 14·1·1·1·14.

*Mastonia ustulata* (Hervier, 1897)

(Pl. 1, Fig. 14)

The operculum is somewhat thick, horny and paucispiral.

All of the radular teeth are almost the same size, attaining  $1.8\mu$  in breadth and height, except the marginals, which are  $1.2\mu$  broad. The radular formula is 21·1·1·1·21. The tricuspoid rachidian tooth is bordered by quadricuspoid laterals and bicuspid marginals.

*Mastonia monilifera* (Hinds, 1843)

(Pl. 1, Fig. 10)

The operculum is thick, horny and paucispiral.

All of the teeth are extremely minute and nearly equal in size, attaining  $1.2\mu$  in breadth and  $1.4\mu$  in height. The rachidian tooth has 3 cusps, of which the median is smaller than the others. The lateral teeth have 4 cusps almost equal in size. The marginals have 2 cusps, of which the outer is larger. The radular formula is 17·1·1·1·17.

*Mastonia conspersa* (Smith, 1875)

(Pl. 1, Fig. 7)

The operculum is horny and paucispiral.

The radular formula is 17·1·1·1·17, the rachidian being tricuspid, the laterals quadricuspid and the marginals bicuspid.

*Viriola tricincta* (Dunker, 1860)

(Pl. 1, Fig. 8; Text figs. 8, 27a, b, c)

The operculum is thin, horny and paucispiral.

The osphradium is rather broad.

The radula consists of numerous rows of minute teeth; the tricuspid rachidian tooth is bordered on each side by quadricuspid lateral and bicuspid marginal teeth, the radular formula being 16·1·1·1·16.

*Viriola connata* (Montrouzier, 1862)

(Pl. 1, Fig. 2)

The operculum is horny and paucispiral.

The tricuspid rachidian tooth is bordered on each side by quadricuspid lateral and bicuspid marginal teeth. The radular formula is 19·1·1·1·19.

*Cantor hungerfordi* (Sowerby, 1914)

(Pl. 1, Fig. 15; Text figs. 25a, b, c, 32)

The operculum is horny and paucispiral.

The tricuspid rachidian tooth is bordered on each side by quadricuspid laterals and bicuspid marginals, the radular formula being 17·1·1·1·17.

*Litharium kurodai* (Kosuge, 1962)

(Pl. 1, Fig. 1; Text fig. 24a, b, c)

The operculum is horny and paucispiral.

The radula consists of numerous rows of minute teeth with the formula 14·1·1·1·14. In each row the pentacuspid rachidian tooth, whose outer cusps are extremely minute, is bordered on each side by a single quadricuspid lateral tooth with small median cusps. The 14 marginal teeth are bicuspid, with cusps of unequal size.

*Cautotriphora pavimenta* (Laseron, 1958)

(Pl. 1, Fig. 4)

The operculum is horny and paucispiral.

The radular formula is 11·1·1·1·11, and consists of the pentacuspid rachidian tooth similar in shape to that reported for *Iniforis concors*, the quadricuspid lateral teeth, and tricuspid marginal teeth.

*Cautotriphora alveolata* (Adams & Reeve,

1850) (Pl. 1, Fig. 9; Text figs. 6, 23a, b, c)

The operculum is horny and paucispiral with 3 whorls.

The proboscis sheath is rather short, continuing to the buccal bulb, which contains the jaw-plates and radula. The jaw consists of 2 scutiform plates, which are covered with numerous fine scales.

The radular formula is 9·1·1·1·9. The number and shape of the cusps of the teeth are as in *C. pavimenta*.

*Cautotriphora hervieri* (Kosuge, 1962)

(Pl. 1, Fig. 11)

The operculum is horny and paucispiral.

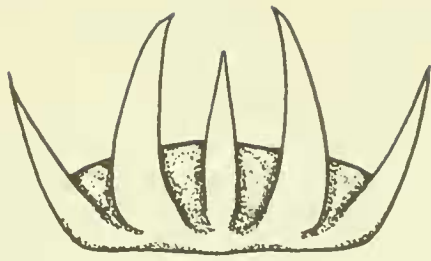
The radular formula is 9·1·1·1·9. The number and shape of the cusps of the teeth are as in *C. pavimenta* and *C. alveolata*.

*Iniforis concors* (Hinds, 1843) (Pl. 1,

Fig. 5; Text figs. 22a, b, c, 31)

The horny operculum has 5 whorls, i.e., is paucispiral.

The mantle cavity is broad and long. The osphradium, also running along the right side of the ctenidium, is narrow and elongate. The proboscis is a broad, multifolded, muscular tube that is rather short when it introverts. The buccal cavity is rather small and not very inflated. The jaw consists of 2 plates which are somewhat obelisc-shaped, tapering to the anterior end, and connected at the dorsal margin. The small and inflated salivary gland enlarges toward the posterior end. It borders on the oesophageal pouch, which runs along the



21 a



21 b



21 c



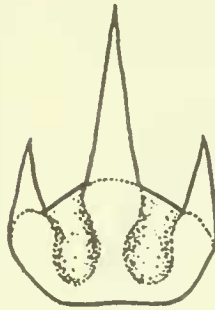
22 c



22 a



22 b



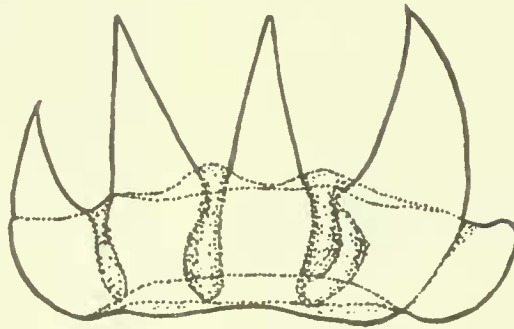
22 b



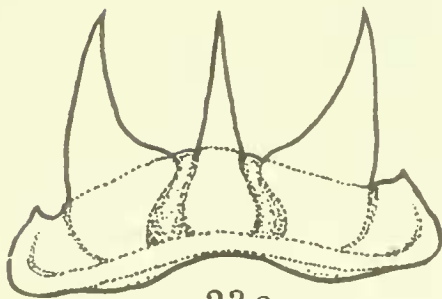
22 c



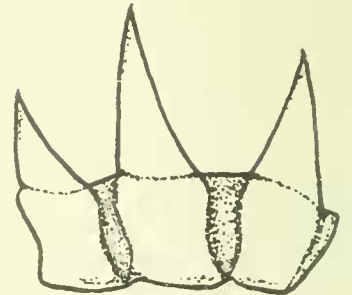
23 c



23 b



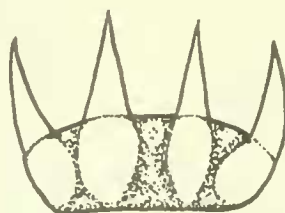
23 a



23 c



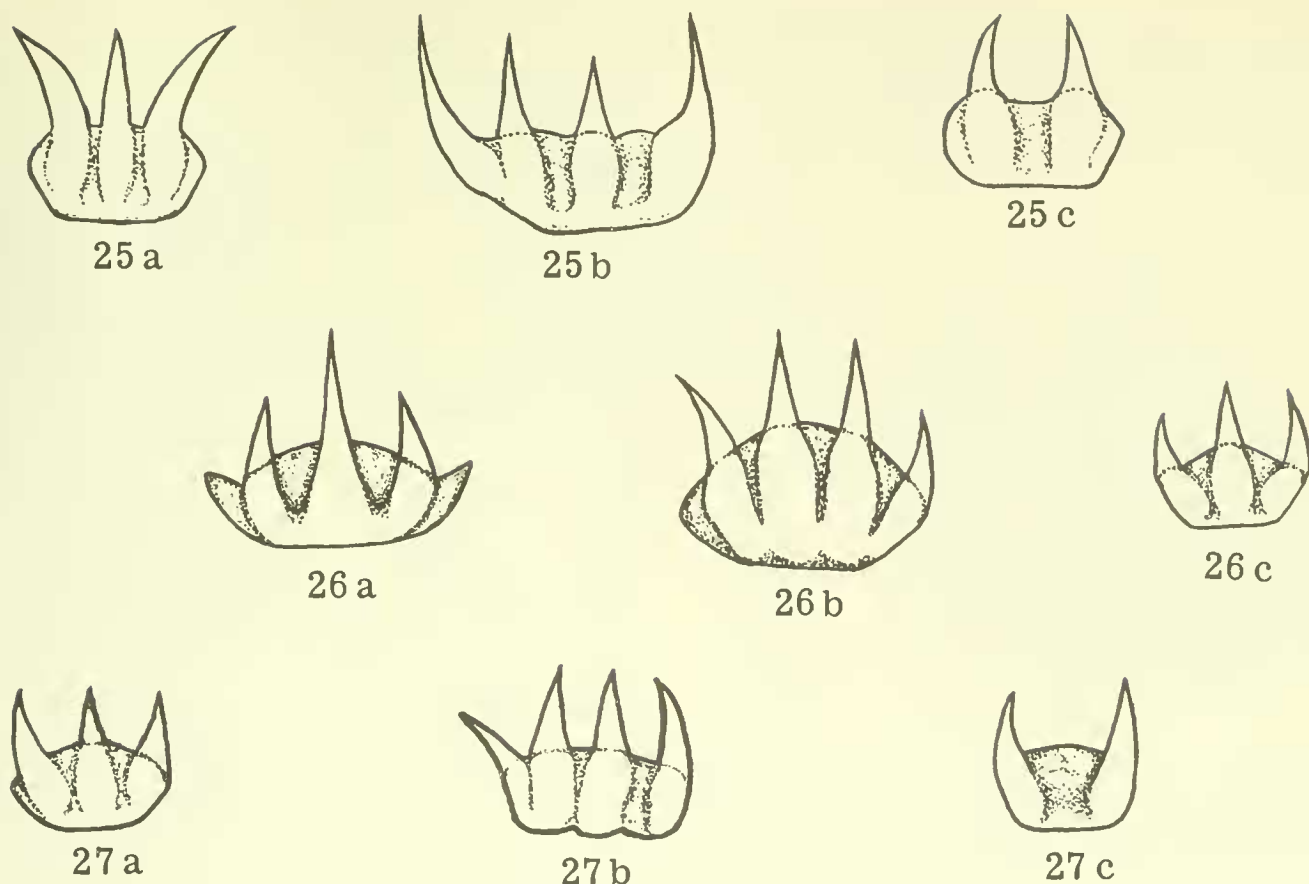
24 a



24 b



24 c



FIGS. 21-27. Radular teeth of some Tripborids: a. rachidian; b. lateral; c. marginal. (Figs. 21-27 drawn to same scale). FIG. 21. *Iniforis albogranosa*. FIG. 22. *Iniforis concors*. FIG. 23. *Cautotriphora alveolata*. (the larger 23c is an inner marginal; the smaller 23c is an outer marginal) FIG. 24. *Litharium kurodai*. FIG. 25. *Cautor hungerfordi*. FIG. 26. *Mastonia rubra*. FIG. 27. *Viriola tricincta*.

oesophagus from the terminal end of the pallial cavity to the front of the stomach. The pallial oviduct is extremely large and occupies the greater part of the posterior mantle cavity.

The radular formula is 7·6·3·6·7, with pentacuspoid rachidians, tricuspoid laterals and unicuspid marginals (compare with typical subfamilial arrangement in the Iniforinae, Fig. 34).

*Iniforis albogranosa* (Kosuge, 1961)  
(Pl. 1, Fig. 6; Text fig. 21a, b, c)

The operculum is horny and comparatively paucispiral.

The buccal cavity is well inflated. The looping part of the oesophagus is long. The oesophageal pouch is somewhat narrow, forming rather coarse folds in it.

The radular formula is 6·2·3·2·6. The number of cusps on the different teeth parallels that in *I. concors*.

*Triphora otsuensis* (Yokoyama, 1920)

(Pl. 1, Fig. 12; Text figs. 28, 29, 35a, b, c)

The operculum is horny and multi-spiral.

The radular formula is 5·1·1·1·5, each row consisting of multicuspoid rachidian and lateral teeth, and unicuspid marginal teeth. The inner 3 cusps and the outer cusp of the lateral tooth are stronger than the other cusps.

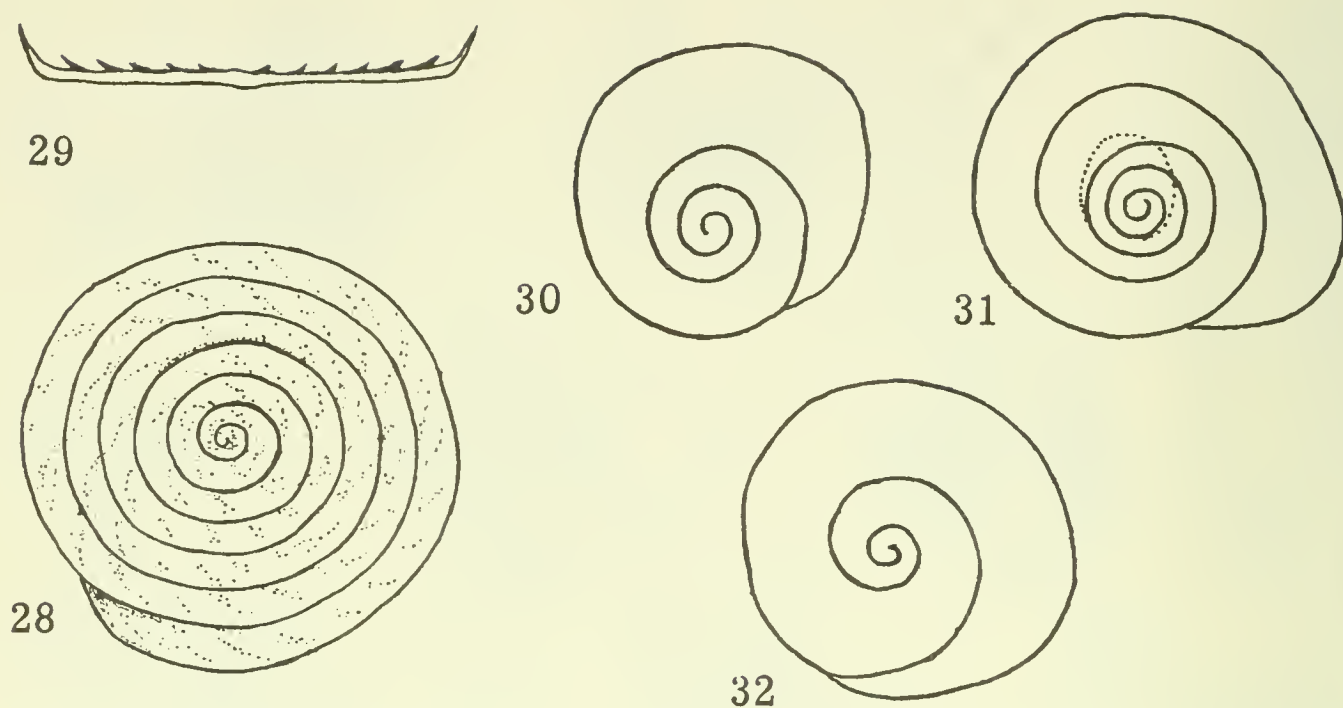
The general features of the soft parts of this species are similar to those reported for *T. perversa*.

#### Shell features in Tripboridae

##### Protoconch

Three types of protoconch are recognized in the Tripboridae.

The 1st type is a narrow conical form of about 5 whorls tapering to the summit.



FIGS. 28-32. Opercula of some Triphorids. FIG. 28. *Triphora otsuensis* (X80). FIG. 29. Same in cross section. FIG. 30. *Cautotriphora alveolata* (X23). FIG. 31. *Iniforis concors* (X23). FIG. 32. *Cautor hungerfordi* (X23).

Each whorl shows a sculpture of 1-2 spiral ridges, crossed by numerous axial threads, resulting in a sort of mesh-work. This sculpturing is common to many members of the family and can be used only as a feature for specific discrimination.

The 2nd type of protoconch is short and few-whorled; it sometimes has a mammillate apex that is rather smooth and sometimes weakly crenated either spirally or axially. This protoconch is taken as a generic characteristic of *Cautor*, *Sychar* and *Epiforis*.

In the 3rd type of protoconch the sculpture usually has the same type of granules as the adult whorl throughout; in some species, the top of the initial whorl is slightly smooth. The protoconch is completely immersed in the shell. This type occurs in the genus *Litharium*.

The smooth, glossy and subulate protoconch, so common in the family Cerithiopsidae, whose shells resemble those of the Triphoridae, was not detected in any of the triphorid species.

#### Shell sculpture

The shell sculpture of the family is of primary importance, both specifically and generically. It consists of spiral rows of granules or of smooth spiral cords. Some species have both granules and smooth ridges mixed. The number of granular rows, ranging from 2-4 on each whorl, has been considered as a definite feature of each genus, e.g., the group having 2 rows of granules is represented by the genus *Maſtonia* (compare Pl. 1, Figs. 3, 7, 13, 14) and the arrangement with 3 rows is widely seen in *Triphora* and other genera (e.g., Pl. 1, Figs. 9, 11, 12). Laseron (1958) proposed the genus *Tetrphora* for species with 4 rows of granules. However, the granular rows are sometimes variable in number. For instance, there is sometimes a minute row of granules between 2 other rows; also, in the group with 3 rows, the median row is narrower and obscure on the earlier whorls of the spire.

The spiral cords are the most essen-

TABLE 1. Radular measurements, in micra; of 16 Japanese Triphorids

Species	Rachidian tooth		Lateral tooth		Marginal tooth	
	Breadth	Height	Breadth	Height	Breadth	Height
<i>Mastonia limosa</i>	1.8	1.2	1.8	1.2	1.2	1.0
<i>Mastonia rubra</i>	3.6	2.4	4.8	2.4	3.0-1.2	1.8
<i>Mastonia undata</i>	3.0	1.4	2.4	1.4	1.2	1.4
<i>Mastonia ustulata</i>	1.8	1.8	1.8	1.8	1.2	1.8
<i>Mastonia monilifera</i>	1.2	1.4	1.2	1.4	1.2	1.4
<i>Mastonia conspersa</i>	5.0	2.4	3.6	2.4	2.4	2.4
<i>Viriola tricincta</i>	4.2	5.1	5.1	5.1	4.2-4.0	5.1
<i>Viriola connata</i>	1.4	1.8	1.8	1.8	1.2	1.2
<i>Cautor hungerfordi</i>	2.4	3.0	3.0	3.0	1.8	2.4
<i>Litharium kurodai</i>	4.8	3.6	4.8	3.6	4.2-2.4	3.6
<i>Cautotriphora pavimenta</i>	4.8	3.6	6.0	3.6	3.6-2.4	3.0-2.4
<i>Cautotriphora alveolata</i>	20.5	12.8	17.9	12.8	14.0-3.8	12.8-5.1
<i>Cautotriphora hervieri</i>	10.2	5.1	10.2	5.1	7.6-2.5	5.1
<i>Iniforis concors</i>	5.4	3.0	4.8-3.0	4.2-3.6	4.2-3.0	12.0
<i>Iniforis albogranosa</i>	4.2	3.0	3.0	2.4	2.4	9.0
<i>Triphora otsuensis</i>	12.0	3.6	8.7	3.0	2.5	15.0

tial characteristic feature of the genus *Viriola* (Pl. 1, Figs. 2, 8). A distinctive sculpture is also found in the genera *Inella* and *Euthymella*; in both, the granules are few in number, spirally elongate, and overridden by spiral ridges.

#### Shell aperture

A remarkable feature of the Triphoridae are the well developed anterior and posterior canals situated at the upper and lower portions of the shell aperture. After the formation of the body whorl is completed, 2 types of siphonal aperture may be discriminated.

In the 1st type of aperture, the anterior siphonal canal varies from a shallow groove to a well developed canal; the anterior margin of the outer lip of the shell aperture is thin and bent in a sharp fold, which develops into a narrow spur. This spur may either fall short of, or reach, the columella and does then partially or completely enclose the anterior siphonal canal, so that the canal opens within the aperture. Externally the anterior siphonal canal may be prolonged into a comparatively long tube. The posterior siphonal canal

is a shallow sinus or, at most, a narrow slit; or it may be an almost circular orifice connected to the outer margin of the shell aperture by a narrow slit. The degree of development of the siphonal canals in species of this type can never be used as a generic or specific feature.

In the 2nd type, the shell aperture may be extended into a circular tube of considerable length. The anterior and posterior siphonal canals are also tubular and more or less enclosed. The appearance of the shell in this 2nd type is very striking; 3 tubes project from the base of the spire, which are sometimes nearly equal in size ("3-mouthed" aperture). Apertures of this type are found in species of *Iniforis* and *Epi- foris*.

#### THE TRIPHORID GROUPS

Jousseume (1884) attached great importance to the shell aperture, and divided the Triphoridae into several groups because of its varying development after maturity. Conversely, Tryon (1887) considered that the condition of the posterior and anterior siphonal canal, i.e.,

whether they are slits or enclosed tubes, depends merely on the growth stage of each individual, and accorded them no systematic value. They are, without doubt, somewhat changeable in accordance with shell growth; however, the enclosed tubular posterior canal, tubular to a greater or lesser extent, is characteristic for a few restricted genera, such as *Iniforis* and *Epiforis*. In these, the radulae are also very distinct and the type of radula found in a species of *Iniforis* and *Epiforis* can be correlated with the tubular character of the posterior siphonal canal.

There are 3 distinct types of radula in the Triphoridae, differing not only in formula, but in the number of cusps of the teeth. Taking into consideration the various points discussed above, but mainly using the radulae and opercula, the following 4 groups can be recognized.

*The 1st group* contains 3 species: *Triphora perversa*, *T. nigrocincta* and *T. otsuensis*. *T. perversa*, which is common in West African, European and Arctic waters, has been studied by Fischer (1887), Fretter (1951) and Johansson (1953). *T. nigrocincta*, from South America, has been investigated by Marcus & Marcus (1963). *T. otsuensis*, commonly occurring on the Japanese coast, has been examined by Kosuge (1964) and is redescribed here.

The radular formula of this group is 5-8·1·1·1·8-5. In *Triphora perversa* the octocuspoid rachidian tooth is bordered on each side by lateral teeth also having 8 cusps, and 8 marginal teeth from which arise 4 narrow elongated cusps. In *Triphora nigrocincta*, the shape and number of teeth is similar to that in *T. perversa*, although the number of cusps differs in that the rachidian has 11 cusps and the marginals are simple. In *Triphora otsuensis* (see Fig. 35, radula given as typical for Triphorinae), the rachidian tooth has 14 cusps of which the outer cusps are larger than the others; the lateral teeth have 12 cusps, of which the inner 3

cusps and outer 1 are rather large. There are 5 unicuspid marginals. The operculum of this group is horny and multispiral (see Fig. 28).

*The 2nd group* contains no species found on the Japanese coast, but contains *Triphora montrouzieri* (Hervier), which is common on the New Caledonian coast. Risbec (1943) investigated this species and reported the radular formula to be  $n' \cdot n \cdot 3 \cdot n \cdot n'$  ( $n=5-7$ ,  $n+n'=13$ ). The rachidian tooth is pentacuspoid; its median cusp is the largest. The tricuspid lateral teeth are rather large, the unicuspid marginal teeth are narrow and elongate. The operculum is horny and multispiral, similar to that found in the 1st group.

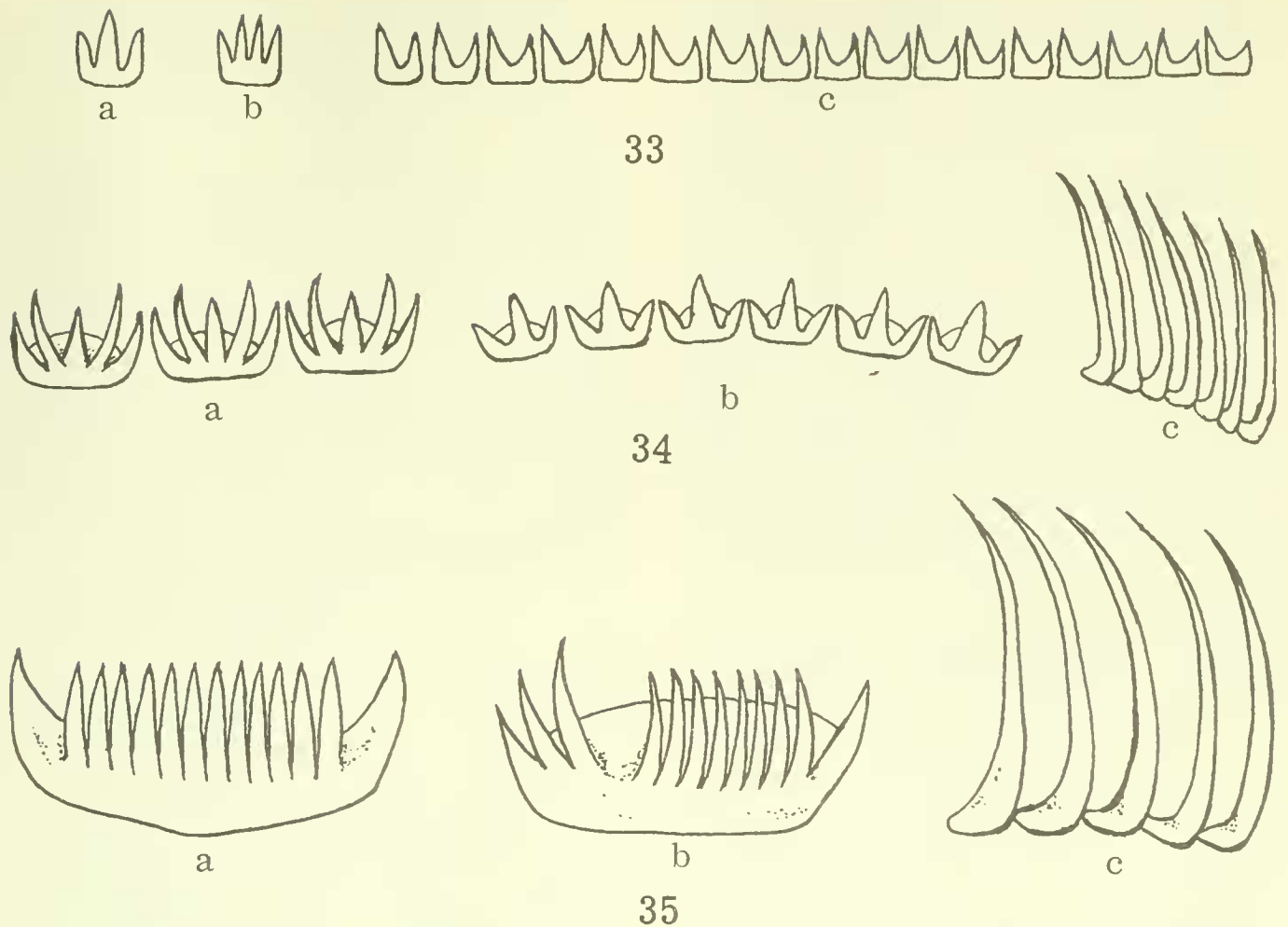
*The 3rd group* includes *Iniforis concors* and *I. albogranosa*, both commonly found on the Japanese coast. The radular formula is 7-6·6-2·3·2-6·6-7, and each denticle is similar to that of the 2nd group in both shape and number of cusps (see Fig. 34). The operculum of this group, with 5 whorls, is paucispiral (see Fig. 31) in contradistinction to the multispiral opercula of the former 2 groups.

*The 4th group* is the most common and contains many species belonging to such genera as *Mastonia*, *Inella*, *Cautotriphora*, *Litharium*, *Cautor* and *Viriola*. The radular formula of this group is  $n \cdot 1 \cdot 1 \cdot 1 \cdot n$  ( $n=9-30$ ). The rachidian tooth has 3 or 5 cusps, of which the median cusp is largest. The lateral teeth are quadricuspoid. The marginal teeth have 2-3 cusps, which are variable in size and number in each species. The operculum of this group is paucispiral, as that of the 3rd group (see operculum of *Cautor*, Fig. 32).

#### Relations among the Triphorid groups

The digestive, nervous and reproductive organs of all groups are similar, while the shell characters, opercula and radulae are different in each group. A striking feature in the radulae is a general tendency for a decrease in the number of cusps in the 3 types. Cooke





FIGS. 33-35. Radulae typical for triphorid subfamilies (not drawn to scale); half a transverse row; a. rachidian(s); b. lateral(s); c. marginals. FIG. 33. Some Mastoniinae, as exemplified by *Mastonia limosa*; the number of marginals varies in the group; some forms have more cusps: a=5 and c=3. FIG. 34. Iniforinae, as exemplified by *Iniforis concors*. FIG. 35. Triphorinae, as exemplified by *Triphora otsuensis*.

(1921) reported a similar decrease in the Volutidae, suggesting that the more advanced species had fewer cusps. It is here assumed that the ancestral, primitive forms had both numerous teeth and cusps, and that various types emerged from them through differential loss of these features.

In the Mesogastropoda, the paucispiral operculum occurs more frequently in the groups of higher rank and this type of operculum is taken to be more advanced than the multispiral type (Hedley, 1917; Taki, 1950). From this point of view, the 3rd group with its paucispiral operculum may be more advanced than the 2nd, in spite of the fact that the radulae of the 2 groups are of the same type, with

teeth and cusps similar in shape and number.

The 4th group is considered to be the most advanced type, both on the basis of the radula as well as on its paucispiral operculum. Its many variable species are distinguished from the other groups by the general reduction in the number of cusps of various teeth, even though the number of marginals is larger. The most primitive group is the first. Its radula, though it has the fewest teeth, has multicuspids rachidian and lateral teeth and sometimes marginal teeth, while the multispiral operculum also is a primitive feature.

Arranging the 4 groups into subfamilies by the nature of their radulae,

and since the radulae of the 2nd and 3rd groups have the same pattern, the author recognizes 3 new subfamilies.

The radular formula of the 1st group is 8-5·1·1·1·5-8 (Fig. 35), the number and shape of teeth are characteristic of the subfamily Triphorinae. The radular formulae of the 2nd and 3rd groups are 7-6·6-2·3·2-6·6-7 (Fig. 34), an essential feature of the subfamily Iniforinae. The 4th group has the radular formula 30-9·1·1·1·9-30, the number and shape of the teeth (with some variation in the number of cusps) being primary features of the subfamily Mastoniinae (Fig. 33).

#### REVISED LIST OF TRIPHORIDAE

Adding the shell characters to the above mentioned features, 11 genera are recognized in these 3 subfamilies, which are treated in the sections to follow. The genera *Epiforis*, *Sychar* and *Inella* are not yet examined, but their shell features, although unique, show such close affinities to other genera examined, that they are included in the following list, in spite of the lack of anatomical information.

Genera such as *Tetraphora*, *Teretriphora* and *Liniphora*, which also have peculiar shell features, may be valid genera; but, as their systematic status cannot be determined exactly by their shell features alone, and as information on their soft anatomy has not yet been obtained, they are omitted from this systematic list.

#### Superfamily Triphoroidea Family Triphoridae

##### Subfamily Iniforinae (Subfam. nov.)

Shell sinistral, acuminate at the summit, and narrowed at the base. The anterior and posterior siphonal canals are usually closed and tubular. The radular formula is  $n' \cdot n \cdot 3 \cdot n \cdot n'$  ( $n'+n=8-13$ ,  $n=2-7$ ); the rachidian has 5 cusps, the laterals have 3 and the marginals are unicuspid.

Genus *Iniforis* Jousseaume, 1884  
syn. *Contraforis* Laseron 1958  
Type species: *Iniforis malvaceus*  
Jousseaume, 1884

Shell sinistral, narrow and acuminate at the summit. The anterior and posterior siphonal canals are tubular and entirely closed (3-mouthed aperture). The shell sculpture consists of 2-3 spiral rows of granules. The radular formula is 7-6·6-2·3·2-6·6-7. The rachidian tooth is pentacuspoid; the lateral teeth are tricuspoid and the marginals unicuspid. The operculum is comparatively paucispiral.

Remarks: The radula, operculum and soft anatomy of the type species *Iniforis malvaceus*, are not known. However, I have examined 2 species, *I. albo-granosa* and *I. concors*, both of which are placed in this genus because of the similarities of their shells to that of *I. malvaceus*. *Iniforis concors* was originally described as a member of the subgenus *Ino* (= *Inella*) of the genus *Triphora*. Because of the differences in shell characters between *Iniforis concors* and *Inella gigas* (type species of *Inella*), it is more reasonable to place these 2 species in different taxa.

##### Genus *Risbecia* gen. nov.

Type species: *Triphora montrouzieri*  
Hervier, 1897

Shell sinistral, acuminate at the summit and narrowed at the base. The anterior siphonal canal is a closed tube; the posterior siphonal canal is a narrow groove. The whorls have 2-3 spiral rows of granules. The radular formula is  $n' \cdot n \cdot 3 \cdot n \cdot n'$  ( $n=5-7$ ,  $n+n'=13$ ). The rachidian tooth is pentacuspoid, the lateral teeth are tricuspoid and the marginals unicuspid. The operculum is multispiral.

Remarks: Hervier (1897) described *Risbecia montrouzieri* as a member of *Inella*, although its shell sculpture differs and the shape of the radula resembles that of *Iniforis*. This species clearly

does not belong in the genus *Inella* as presently understood, but it has never been placed with any other group. There are certain distinct differences between *R. montrouzieri* and species of *Iniforis*, in spite of their similarity of the radula, viz., the operculum of *R. montrouzieri* is multispiral and the posterior siphonal canal is not a closed tube. Since the operculum and radula are different from those of any other group, a new genus *Risbecia* is proposed here. It is dedicated to Dr. J. Risbec, the first to report the precise anatomy of *Risbecia montrouzieri*.

Genus *Epiforis* Laseron 1958

Type species: *Epiforis australis*  
Laseron, 1958

Shell sinistral, conical with a somewhat convex spire, restricted at the base. The anterior and posterior siphonal canals are well developed and tubular. The whorl sculpture consists of 2 spiral rows of granules. The protoconch is short, broad and cylindrical without apparent axial threads. The radula, operculum and the soft anatomy are unknown.

Remarks: This genus is separated from *Iniforis* only by the protoconch.

Subfamily Mastoniinae (Subfam. nov.)

Shell sinistral, acuminate at the summit, and narrowed at the base. The anterior and posterior siphonal canals are narrow grooves. Each whorl bears 2-3 rows of spiral ridges or granules. The radular formula is  $n \cdot 1 \cdot 1 \cdot 1 \cdot n$  ( $n=9-30$ ). The rachidian tooth has 3 or 5 cusps, the laterals have 4 and the marginals 2 or 3 cusps. The operculum is comparatively paucispiral.

Remarks: Characters of special importance in distinguishing this subfamily from the subfamily Iniforinae are the number of radular teeth and their cusps (compare Figs. 33 and 34).

Genus *Mastonia* Hinds 1843

Type species: *Triphora vulpina*  
Hinds, 1843

The spire is inflated and rather spin-

dle-shaped. Each whorl has a spiral sculpture of 2 rows of granules. Sometimes there is an intermediate row of minute granules. The rachidian tooth has 3 or 5 cusps, the lateral teeth have 4 and the marginals 2 or 3 cusps.

Remarks: Among the species which Hinds reported as members of this genus, *Mastonia rubra* and *M. monilifera* have been examined in the present study; in addition also *M. undata*, *M. ustulata* and *M. conspersa*. The radulae and opercula of this genus are similar to those found in other genera of the subfamily; however, the radulae are so minute that the rachidian tooth can hardly be distinguished from the others. Other generic features are the sculpturing, which shows 2 spiral rows of granules on each whorl, the spindle shaped shell, and the posterior siphonal canal with a narrow, not completely closed slit.

Genus *Inella* Bayle 1878

Type species: *Triphora gigas*  
Hinds, 1843

Each whorl is adorned with 3 spiral rows of granules, the granules being interconnected by spiral and axial cords. The protoconch is blunt, dome-shaped and bears a few spiral ridges.

Remarks: The rather large and narrow, acuminate, conical shell and the sculpture are somewhat like those of *Viriola* and are closely allied to the Japanese species *Cautotriphora pyramidalis* and *C. alveolata*. However, the radula is larger and the rachidian tooth has more cusps than are found in the other genera. The soft anatomy of *I. gigas* is not yet known.

Genus *Cautotriphora* Laws 1940

Type species: *Notosinister simulans*  
Laws, 1940

Shell sinistral, elongated, subulate-conical with a somewhat straight spire. The protoconch is subulate, conical, with a sculpture of fine spiral and axial threads. Each whorl has 3 spiral ridges evenly and regularly nodulated. These nodules are connected axially by ridges

that are weaker than the spirals, giving a fenestration of squares. The rachidian is pentacuspoid, the laterals are quadricuspoid and the marginals tricuspoid.

Remarks: Three species belonging to this genus were examined by the author: *C. alveolata*, *C. pavimenta* and *C. hervieri*. The protoconch of this genus is subulate, but differs in type from that of *Inella gigas*. Other shell features of this genus resemble that of *Inella*.

Genus *Litharium* Dall 1924a

Type species: *Triphora oceanida*  
Dall, 1924a

Each whorl shows a spiral sculpture of 3 rows of granules, with the protoconch immersed at the summit. The rachidian tooth is pentacuspoid, the lateral teeth quadricuspoid and the marginals bicuspid.

Remarks: The shell shape and sculpture of this genus is closely allied to that found in *Triphora* and *Cautor*, but the genus differs markedly in its completely immersed protoconch. *L. kurodai* has been assigned to the genus on this latter character, although its radula and operculum agree with those of the genus *Mastonia*.

Genus *Cautor* Finlay 1927

Syn. *Distophora* Laseron 1958  
Type species: *Triphora lutea* Suter,  
1908

Each whorl shows a spiral sculpture of 3 rows of granules. The protoconch comprises 2-3 whorls. It is blunt and either mammillate or nearly smooth. The rachidian tooth is tricuspoid, the lateral teeth are quadricuspoid and the marginals are bicuspid.

Remarks: The shell and sculpture are very similar to that of *Litharium*, but *Cautor* is easily distinguished from other genera by its smooth or mammillated protoconch, its only distinctive feature. The soft anatomy of the Japanese species, *C. hungerfordi* belonging to this genus, is similar to that of *Mastonia*.

Genus *Viriola* Jousseume 1884

Syn. *Orbitophora* Laseron 1958  
Type species: *Triphora bayani*  
Jousseume, 1884

Each whorl has a spiral sculpture of smooth ridges. The protoconch is a subulate cone with a sculpture of fine axial and spiral threads. The rachidian tooth is tricuspoid, the lateral teeth are quadricuspoid and the marginals are bicuspid.

Remarks: This genus has hitherto been referred to a distinct subfamily Viriolinae by reason of its unique sculpture. However, the shape and number of teeth of *Viriola* is the same as that of other Mastoniinae and it is therefore inappropriate to treat it as a distinct subfamily. The species examined by the author are: *V. tricineta* and *V. connata*.

Subfamily Triphorinae (Subfam. nov.)

As the subfamily is monogeneric, the genus description stands for the subfamily.

Genus *Triphora* Blainville 1828

Syn. *Notosinister* Finlay 1927  
Type species: *Triphora gemmata*  
Blainville, 1828

Shell sinistral, elongate and narrow, acuminate towards the apex and narrowed at the base. The anterior siphonal canal is a narrow groove and the posterior siphonal canal forms a narrow slit. The whorls show a spiral sculpture of 3 rows of granules. The radular formula is  $n \cdot 1 \cdot 1 \cdot 1 \cdot n$  ( $n=5-8$ ). The rachidian tooth and the lateral teeth are broad, with many cusps. The marginal teeth are unicuspid or may have several cusps. The operculum is multispiral.

Remarks: *Triphora perversa* (Linné) is closely allied to the type species by its shell features and has been treated as a member of this genus by Thiele and others. Its anatomical features have been carefully studied by various authors.

The radula is very distinct and has no similarity to other forms in the family, although the shell sculpture, which consists generally of 3 equal rows of granules, and the protoconch, are somewhat similar to those occurring in other taxa. Other species of the genus *Triphora* as here defined are *T. nigrocincta* and *T. otsuensis*. Since the species of *Notosinister* examined by the author (1964) were found to have the same type of radula and operculum as *T. perversa*, *Notosinister* is treated as a synonym. Originally *Cautotriphora* was proposed as a subgenus of *Notosinister*, but its shell features do not warrant such a position.

Laseron (1958) used the generic name *Triphora* for the species which have a closed tubular posterior siphonal canal, but these species also differ from *Triphora* as here understood in their radula and operculum. Species with such a character may belong to the genus *Iniforis* or *Epiforis*.

#### RELATIONSHIPS WITHIN THE TRIPHORIDAE

The genus *Triphora* may be considered a primitive type, because of its multi-spiral operculum and the shape of the radula, in particular the great number of cusps of its rachidian and lateral teeth, and it is thought to have directly branched off from the ancestral stock. It is somewhat difficult to account for the relations between the genera *Risbecia* and *Triphora*, whose radulae differ greatly, being of the types  $n' \cdot n \cdot 3 \cdot n \cdot n'$  and  $n \cdot 1 \cdot 1 \cdot 1 \cdot n$  respectively, with *Risbecia* having few cusps only in the rachidian and lateral teeth. Perhaps the similarity of the marginal teeth and opercula may give a clue to their affinities. Cooke (1921) is of the opinion that the cusps of the teeth in the Volutidae decreased in number with progressing evolution. A similar reduction in the cusps may have taken place in the family Triphoridae.

Since the genus *Iniforis* has a radula

similar to that of *Risbecia*, it is not unreasonable to assume that *Iniforis* is closely related to and perhaps derived from that genus, although it differs in its operculum. The shell features of the genus *Epiforis* indicate that it is closely allied to the genus *Iniforis* except for the protoconch and, in spite of the lack of information on the soft anatomy of *Epiforis*, the 3 genera (*Risbecia*, *Iniforis* and *Epiforis*) may perhaps be placed in the same group (Iniforinae).

The forms here placed in the subfamily Mastoniinae must be considered another branch of the family. Their radula ( $n \cdot 1 \cdot 1 \cdot 1 \cdot n$ ) is different from that of the Iniforinae; the single rachidian and lateral teeth, though of a similar type, differ in number, while the marginals differ in both the number of the teeth and their cusps.

*Cautotriphora* seems to be closely related to *Triphora* and *Risbecia* in sculpture and in the low number of rachidian and lateral teeth, whose size and shape in *Cautotriphora* is somewhat parallel to that in *Risbecia*. The sculpture of *Cautotriphora* and *Inella*, which consists of spirally nodulated ridges, are rather like that of *Viriola*, especially in its arrangement of the spiral ridges. Furthermore, the radula and operculum are of the same type, giving further indications of their close affinities. In view of its radula and operculum, the genus *Mastonia* may be considered to have been derived from *Cautotriphora*.

The relations of the 11 recognized genera are suggested in Fig. 36.

#### RELATIONS OF THE TRIPHORIDAE TO OTHER FAMILIES

The Triphoridae have been hitherto referred to the mesogastropod superfamily Cerithioidea on the basis of their shell features, but the characteristics of the animals do not permit the family to remain in that superfamily.

Within the Cerithioidea, the family Cerithiopsidae has been considered the group most closely related to the Tri-

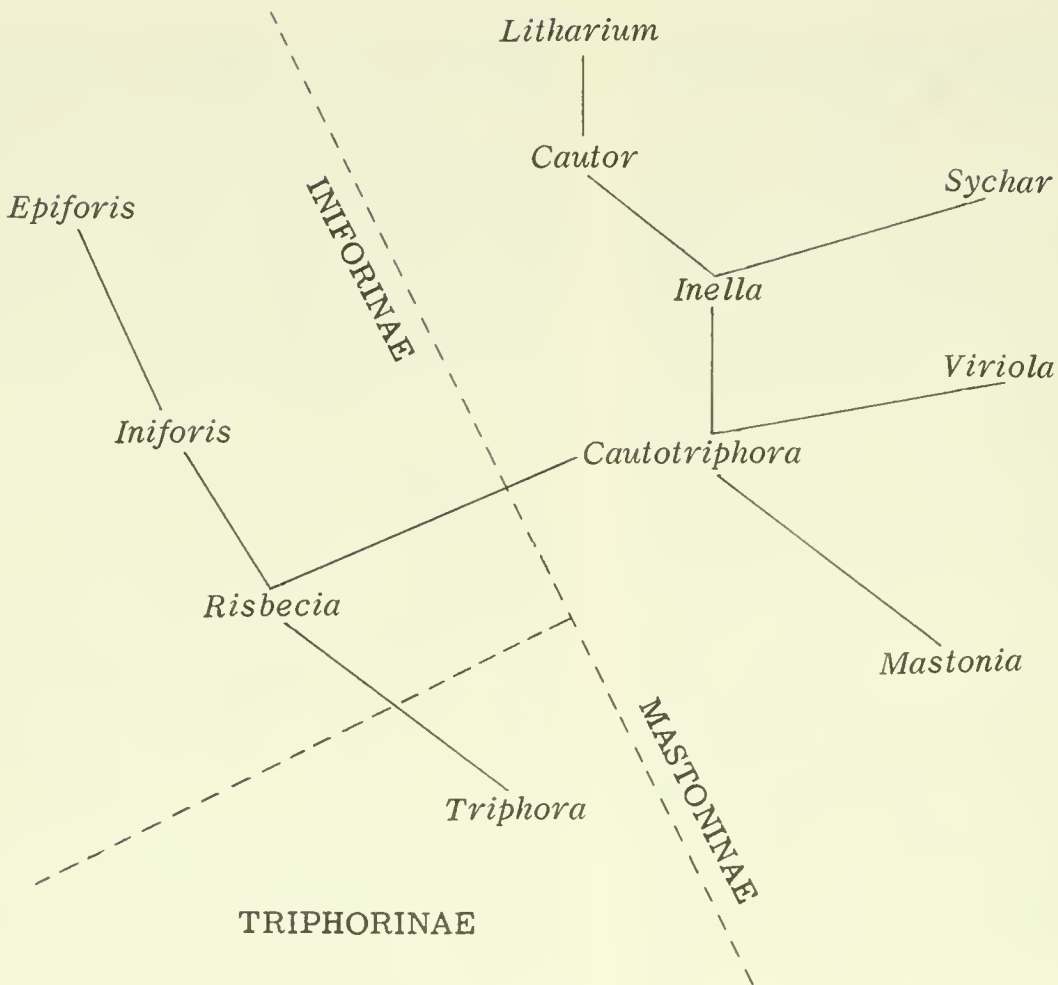


FIG. 36. Probable phylogenetic relationships in the family Triphoridae.

phoridae from the viewpoint of their shell features, especially the sculpture. In fact, because the same pattern of sculpture is found in both families, although the coiling of the shell is reversed, some authors have treated them as a single family. The Cerithiopsidae also have similar feeding habits. However, the Triphoridae differ from the Cerithiopsidae in radula, protoconch, operculum and features of soft anatomy.

The radula of the Cerithiopsidae is a typically taenioglossate one, with the formula 2·1·1·1·2. The shapes of the cusps in this family are also very different from that in the Triphoridae, which are minute and not so prominent as those of the Mesogastropoda (Taenioglossa).

The protoconch of the Cerithiopsidae is smooth and vitreous, and has few whorls, thereby differing from the mul-

tispiral sculptured or mammillated protoconchs of the Triphoridae. The operculum of the Cerithiopsidae is peculiar for a member of Mesogastropoda in that it is lamellated. It also differs in certain details from the lamellated form found in the neogastropod *Stenoglossa*, and may be distinct from that of both *Taenioglossa* (=Mesogastropoda) and neogastropod *Stenoglossa*.

The Triphoridae similarly differ from the family Cerithiidae: the protoconch of the latter is smooth and has few whorls, being more closely allied to the cerithiopsid than the triphorid protoconch; the radula of the Cerithiidae is also typically taenioglossan.

Risbec (1943) and Fretter (1951) have pointed out that the proboscis of the Triphoridae is acrembolic, i.e. the buccal cavity and buccal ganglia are situated in the terminal part of the proboscis

sheath; when the proboscis introverts, they are placed in the posterior part of the haemocoel. But the buccal arrangement of the Cerithiidae and Cerithiopsidae, where the buccal mass is placed behind the mouth opening is entirely different. Nor has the oesophageal pouch, a most characteristic organ of the Triphoridae, ever been found in these 2 families. The acrembolic proboscis is another characteristic feature of the Triphoridae, which is widely seen in the Mesogastropoda, and gives some clue to the systematic position of the family. This type of proboscis is not found in the stenoglossan prosobranchs.

Pallial tentacles, present in triphorids (as in rissoids and Epitoniacea), are lacking in cerithiids.

The Triphoridae also differ from other groups of Cerithioidea in the points mentioned above. Therefore the family can no longer be considered a member of that superfamily and needs to be transferred to another more suitable systematic position.

Risbec (1955) advocated the removal of the Triphoridae from the Cerithioidea, because of similarities in radula and digestive organs to the stenoglossan family Columbelloidea, and the establishment of a special group intermediate between the Mesogastropoda and the neogastropod Stenoglossa. He considered the position of such a group to be closer to the Columbelloidea than to the Cerithioidea. Although I concur with the establishment of such an intermediate group, I do not with its position close to the Columbelloidea.

The Triphoridae differ from the neogastropod Stenoglossa in the following points: 1) Quite apart from the variation in size and position of the nucleus, the opercula of the Stenoglossa are of a lamellated type in general; other types of opercula, such as the spiral form seen in the Triphoridae, have never been found in that taxon; 2) The proboscis of the Triphoridae is of the acrembolic type never found in Stenoglossa.

The features of the opercula and soft anatomy of the animal do therefore indicate a place closer to the Mesogastropoda than to the neogastropod Stenoglossa.

From the viewpoint of the radula, the Triphoridae seem to somewhat resemble the Epitoniacea in the reduced number of teeth, although these 2 groups show essential differences in the form and number of the cusps. They also show other resemblances in the digestive tract. Perhaps they have advanced on a parallel course of evolution, each adapting to the mastication and digestion of the particular food on which they preferably feed.

According to Taylor & Sohl (1962), it has been recognized by various authors that the families Mathildidae and Architectonicidae, related to one another by their heterostrophic protoconch and common features of the radula (Thiele, 1928), do not rightly belong in the Cerithioidea, where they were placed by Thiele. Following Ovechkin and Pchelintsev, they list the Architectonicidae, along with "? Omalaxidae", in a separate mesogastropod superfamily (Architectonicacea) and note Risbec's (1955) opinion, that this family had more in common with the euthyneuran Pyramidelloidea than the Cerithioidea.

Resemblances of the Architectonicidae with the Triphoridae in the digestive tract lie especially in their acrembolic type proboscis, which results in a posteriorly situated buccal cavity. The jaw plates of the 2 families are of the same pattern. The radula also differs from typical Taenioglossa in shape of the teeth and cusps. The Architectonicidae therefore seem to be a group related to the Triphoridae, both being derived from the same ancestral stock.

The allied Mathildidae have shells of a pattern and sculpture closely similar to the Triphoridae.

In conclusion, believing that the Triphoridae should be transferred from the superfamily Cerithioidea, I proposed and established, in 1964, a new superfamily,

the Triphoroidea. This new superfamily is a group intermediate between Mesogastropoda (Taenioglossa) and the neogastropod Stenoglossa. Here, a new subordinal group, which includes the families Triphoridae, Mathildidae and Architectonicidae, and also the Epitonioidae (Ptenoglossa) is distinguished from both Mesogastropoda and the neogastropod Stenoglossa. Heterogastropoda is proposed as a name for this new suborder (Ref. Habe & Kosuge, 1966).

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## RESUMEN

## LA FAMILIA TRIPHORIDAE Y SU POSICION SISTEMATICA

Los Triphoridae fueron hasta ahora referidos a los Cerithioidea en base a caracteres concológicos, aunque algunos autores recientes han señalado que esta familia difiere de las otras en la superfamilia, por su rádula, sistema digestivo y opérculo. Este trabajo trata las especies japonesas, que se colocan en tres grupos basados en sus rádulas y opérculos. Risbec (1943) reconoce cuatro grupos en la entera familia.

El 1<sup>er</sup> grupo tiene opérculo multispiral. La fórmula radular es 8-5·1·1·1·5-8. El diente raquídeo, y laterales son multicúspidos y los marginales unicúspidos. El grupo esta representado por la común especie europea *Triphora perversa* la sudamericana *T. nigrocincta*, la japonesa *T. otsuensis*, y varias especies de *Notosinister* del Japón.

El 2<sup>o</sup> grupo tiene el mismo opérculo que el primero, pero su fórmula radular es 7·6·3·6·7. Tres raquídeos pentacúspidos estan flanqueados por laterales que difieren de ellos por tener solo tres cúspides. Los marginales son unicúspidos, como en el 1<sup>er</sup> grupo. Una nueva especie de Caledonia, *T. montrouzieri*, y otras especies indeterminadas de *Triphora* incluidas por Risbec, pertenecen a este 2<sup>o</sup> grupo.

El 3<sup>er</sup> grupo tiene el mismo tipo de rádula que el 2<sup>o</sup>, pero el opérculo es comparativamente paucispiral (5 vueltas), diferente de los otros dos grupos. Incluye formas con abertura tridentada, como *Iniforis concors* e *I. albogranosa* comunes en el Indopacífico.

El 4<sup>o</sup> grupo tiene opérculo paucispiral similar al 3<sup>er</sup> grupo. La fórmula radular es n·1·1·1·n (n=9-30): el raquídeo tiene 3-5 cúspides. Incluye la mayoría de las especies de *Mastonia*, *Inella*, *Litharium*, *Cautotriphora* y *Viriola*.

Se revisan los géneros y secciones hasta ahora conocidos de Triforidos. Ciertos número de formas fueron recombinadas desde el punto de vista anatómico y concológico, en tres familias: Triphoridae (grupo I), Iniforinae (grupos II y III) y Mastoniinae (grupo IV), de los cuales los Triphorinae se consideran los más primitivos y los Mastoniinae los más avanzados. Se reconocen 11 géneros, más uno nuevo, *Risbecia*, propuesto para *T. montrouzieri*.

De acuerdo a los rasgos del sistema digestivo, tales como la proboscis acrembolica, la presencia de un saco esofágico, rádula, y opérculo espiral (no lamelado), no puede mantenerse la ubicación de la familia Triphoridae en la superfamilia esencialmente tenioglosida de los Cerithioidea, ni tampoco colocarla entre los neogastropodos del suborden Stenoglossa. Por estas razones el autor ha establecido una nueva super-

familia Triphoroidea en el suborden Mesogastropoda, y ubicada cerca de la superfamilia Epitonioidae (Ptenoglossa). Además, un nuevo suborden, los Heterogastropoda, que incluye los Triphoridae, Mathildidae, Architectonicidae y Epitonioidae (Ptenoglossa), que se distingue de ambos los Taenioglossa y los Stenoglossa.

## АБСТРАКТ

## СЕМЕЙСТВО TRIPHORIDAE И ЕГО СИСТЕМАТИЧЕСКОЕ ПОЛОЖЕНИЕ

Садао Косуге

Благодаря некоторым особенностям строения раковины, семейство *Triphoridae* до сих пор относили к *Cerithioidea*, хотя некоторые современные авторы указывали, что оно отличается от других семейств этого же надсемейства строением радулы, пищеварительного тракта и крышечки. В настоящей статье рассматривается 16 японских видов *Triphoridae*, разделенных автором на 3 группы, в соответствии с устройством их радулы и крышечки. Таким образом вместе с группой, выделенной ранее Рисбеком (1943), в семействе насчитывается 4 группы видов.

Виды первой группы имеют крышечку с большим количеством спиральных оборотов. Формула радулы: 8-5.1.1.1.5-8. Рахидиальные и латеральные зубы несут многочисленные зубчики, каждый маргинальный зуб имеет по одному зубчику. Эта группа представлена обычным европейским *Triphora perversa*, южно-американским *T. nigrocincta* японским *T. otsuensis* и некоторыми японскими видами *Notosinister*.

Виды второй группы имеют крышечку того же строения, но они отличаются строением радулы: 7.6.3.6.7. У них имеется три рахидиальных зуба, с пятью зубчиками на каждом; с каждой стороны к ним примыкают по 6 боковых зубов, которые отличаются от рахидиальных тем, что имеют лишь 3 зубчика. Маргинальные зубы с одним зубцом, такие же как и у видов первой группы. Ко второй группе относятся *T. montrouzieri* - (новый каледонский вид) и другой ее неопределенный до вида представитель р. *Triphora* указанный Рисбеком.

Виды третьей группы имеют радулу того же типа, что у второй (по количеству самых зубов и зубчиков на них), однако их крышечка имеет сравнительно мало оборотов спирали (5), чем и отличается от обеих предыдущих групп. К третьей группе относятся виды с "фигурным треугольным" типом устья раковины, как например, *Iniforis concors* и *I. albogranosa*, обычные для Индо-Тихоокеанской области.

Виды четвертой группы имеют крышечку со сравнительно малым количеством спиральных оборотов, т.е. сходную с крышечкой третьей группы. Формула радулы:  $n.1.1.1.n$  ( $n=9-30$ ); рахидиальный зуб с 3-5, боковые - с четырьмя, а маргинальные с двумя - тремя зубчиками. В эту группу входит большая часть видов *Mastonia*, *Inella*, *Litharium*, *Cautotriphora* и *Viriola*.

В настоящей работе ревизуются все известные в настоящее время рода и секции семейства *Triphoridae*.

Принимая во внимание анатомию и строение раковины, многие формы были распределены в три новых подсемейства: *Triphorinae* (первая группа), *Inforinae* (вторая и третья группы) и *Mastoniinae* (четвертая группа).

Из них *Triphorinae* рассматриваются, как наиболее примитивные, а *Mastoniinae* -- как наиболее развитые формы. В составе семейства насчитывается 11 родов, а для "*Triphora*" *montrouzieri* предлагается новый род *Risbecia*.

Принимая во внимание особенности строения их пищеварительного тракта, таких как акремболический хоботок, наличие глоточных карманов, строение радулы и спиральной (не пластинчатой) крышечки, оказалось невозможным сохранить сем. *Triphoridae* в надсемействе, типичном для *Taenioglossa*. Поэтому автор установил новое надсемейство *Triphoroidea* в подотряде *Mesogastropoda*. Это надсемейство близко к надсемейству *Epitonioidea* из *Ptenoglossa*. Кроме того, новый подотряд, *Heterogastropoda*, включающий *Triphoridae*, *Mathildidae*, *Architectonicidae* и *Epitonioidea* (*Ptenoglossa*) отличается как от *Mesogastropoda* (*Taenioglossa*), так и от *Neogastropoda* (*Stenoglossa*).